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The flexibility of an intermediate feeder: dietary selection by mountain hares measured using faecal n-alkanes

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Abstract Herbivores with an intermediate feeding strategy either vary their diet between a grazing (bulk roughage feeders) or browsing (concentrate selectors) strategy on a seasonal basis or select a mixed diet at any one time. The underlying ecological causes of the seasonal dietary shift in a small non-ruminant intermediate feeder – the mountain or arctic hare (*Lepus timidus* L.) were determined. Diet composition and selection relative to availability were investigated for 41 individual free-ranging mountain hares (of which 18 female hares were radio-collared) occupying an upland mosaic landscape in north-east Scotland. Diet composition was determined using faecal n-alkane analysis. Radio-collared hares were designated as pasture, woodland or moorland hares according to the habitat that predominated their home-range. In common with previous studies, mountain hares switched from a browse-dominated diet during winter to a Gramineae-dominated diet in summer, although it was only significant for reproductively active females during the peak breeding season. Diet composition remained consistent regardless of habitat occupied. However, the diet of radio-tracked hares differed significantly from the biomass available in the individual home-ranges; Gramineae were preferentially selected over browse species throughout the year. During winter and in particular during the early breeding season, intermediate feeders, such as mountain hares, ate browse material when the availability of higher quality was restricted. The ability to browse or graze represents a flexible foraging strategy permitting survival and production through periods of changing or unpredictable forage quality and availability.

Keywords Foraging strategy · Alkane analysis · Radio-telemetry · Grazer-browser · Lagomorph

Introduction

The classification of herbivores along a continuum from concentrate selectors (browsers), through intermediate feeders to bulk roughage feeders (grazers), has dominated studies of mammalian herbivory since it was proposed for ungulates (ruminants) by Hofmann (1968, 1973, 1989). Although the nutritional and physiological functioning underlying these feeding strategies has been questioned (Gordon and Illius 1994, 1996; Robbins et al. 1995), there is little doubt that herbivores fall neatly into this scheme according to their feeding habits (Iason and Van Wieren 1999), and that the classification applies to a range of taxonomic groups (Evans and Jarman 1999). The intermediate feeders are a particularly interesting group since they may simultaneously show characteristics of grazers, eating mainly Gramineae, and browsers, selectively eating parts of woody plants. Alternatively, they may switch between these strategies between seasons (Hofmann 1989), resulting in an equivalent mixed diet when considered on an annual basis. Whether intermediate feeders select a varied diet throughout the year or switch diets between seasons, their ability to digest food maximally may be compromised either because of inadequate adaptation or digestive specialism to the contrasting food substrates (Iason and Van Wieren 1999). In this paper we determine the underlying ecological causes of the seasonal dietary shift in mountain hares (*Lepus timidus* L.), an intermediate feeder.

Like other boreal lagomorph species, the mountain hare in Scotland has often been considered to be a browser, but is now known to be an intermediate feeder, eating mainly Gramineae in summer and heather (*Calluna vulgaris* L. Hull) in winter (Flux 1970; Iason and

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Waterman 1988). *Calluna* is a low growing ericaceous evergreen woody shrub, which is both lignified and rich in phenolic secondary plant metabolites; both of which confer lower digestibility than Gramineae and the phenolics can cause sodium imbalance (Pehrson 1983; Iason and Van Wieren 1999). There are, therefore, several reasons why mountain hares should avoid *Calluna* when alternatives are available. Despite the association of high densities of mountain hares with *Calluna*-dominated moorland in both Scotland and on Swedish coastal islands (Watson et al. 1973; Angerbjörn 1981), it has been demonstrated that, relative to habitat availability, mountain hares avoid *Calluna*-dominated habitats in favour of newly afforested areas, upland pastures or other areas of short moorland vegetation especially those which contain a variety of Gramineae species (Hewson 1989; Hulbert et al. 1996a).

In this study we determine whether the pattern of habitat selection of individual mountain hares, determined by radio telemetry, is reflected in a similar flexibility in diet composition which was determined using the novel method of faecal n-alkane analysis (Dove and Mayes 1991). We also determine whether any changes in diet composition are consistent among hares occupying contrasting habitats thus reflecting different degrees of selectivity maintaining a constant composition. Specifically we test the hypothesis that seasonal dietary shifts associated with the intermediate feeding strategy are simply the result of seasonal changes in the availability of different food plants.

Materials and methods

Study site

The 400 ha study area was located in an upland landscape (Grid Ref NJ345170) in the foothills of the Cairngorm Mountains of north-east Scotland and comprised upland pasture, coniferous woodland and open moorland (Hulbert et al. 1996a). The three land use types were altitudinally stratified with upland pasture between 320 and 450 m above sea level (a.s.l.), coniferous woodland at 350–550 m a.s.l. and moorland at 450–650 m a.s.l. The upland pasture consisted of agricultural Gramineae mixtures dominated by perennial ryegrass (*Lolium perenne* L.) while *Calluna* dominated the vegetation on the moorland. The ground flora in the coniferous woodland was separated into three plant community types: (i.) ericaceous-woodland with a ground flora dominated by *Calluna* and blaeberry (*Vaccinium myrtillus* L.); (ii) rush-woodland with a ground flora dominated by great wood rush [*Luzula sylvatica* (Hudson) Gaudin]; and (iii.) graminaceaous-woodland with a ground flora dominated by wavy-hair grass (*Deschampsia flexuosa* L. Trin.). The woodland tree species were dominated by Sitka spruce [*Picea sitchensis* (Bong.) Carr.] which were 3 m in height and aged 10–12 years. Using aerial photographs verified by ground checking, the boundaries of the different plant community types were digitised using the GIS PC-ARCINFO (Environmental Systems Research Institute 1987).

Trapping of animals

Two-hundred and sixty-eight live-trapping events (118 individual mountain hares) were made between December 1989 and September 1991 using Tomahawk cage traps (Tomahawk, Wis., USA). All animals were weighed, sexed and their age category (leverets or adults) determined by palpation of the epiphyseal notch at the head of the tibia (Flux 1970). For females the presence of mammary tissue was scored on a scale 0=none, 1=low, 2=medium and 3=high. Females were defined as "reproductively" active if successfully palpated for embryos and/or the mammary tissue had a score of 2 or 3. All faeces deposited while the hare was confined within the trap (<8 h) were collected and stored at –20°C within 24 h. Each animal was fitted with individually identifiable eartags and 18 adult females were fitted with Biotrack radio transmitting collars (Wareham, Dorset, UK). Eight of the radio-collared hares were caught either on the moor or at the treeline, seven were caught within the woodland and five caught along a derelict "rabbit-proof" fence separating the woodland and pasture habitats.

Radio tracking

Radio-collared animals were located using portable receivers (Mariner Radar, Lowestoft, England) equipped with a Yagi antenna using triangulation techniques (Kenward 1987). Thirty locations were obtained at random intervals throughout the 24 h cycle from each animal every month for 1–15 months. Each animal was classified as a "pasture", "woodland" or "moorland" hare according to the proportion of locations in their home-range observed on the upland pasture, in the woodland and on the open moorland. Further details of the techniques used are in Hulbert et al. (1996b). The size of home-range and night-range size of each hare was estimated using the Multinuclear Probability Polygon (Kenward 1990). Night-range was defined as the range occupied when hares were active and generally feeding (1901–0500 hours GMT) (Hewson and Hinge 1990) and 10–15 locations were obtained from each animal each month on different nights during this time interval. The night-range of each radio-tracked hare was overlaid onto the digitised map to calculate the available area of each plant community type on an individual animal basis (Hulbert et al. 1996a).

Green biomass availability

The seasonal availability of green biomass (kg DM ha^{-1}) was estimated in December, March, June and September for each plant-community type. Vegetation was clipped at ground level in 9–12 random quadrats (23×55 cm). The number of quadrats varied according to the season, but was determined after plotting the cumulative mean wet weight of each sample against the number of quadrats for the most structurally diverse community (Muller-Dombois and Ellenberg 1974). Every month, each collection sample was sub-sampled and the material separated into live current shoots of Gramineae, sedges, rushes, dwarf shrubs and ericaceous species. All samples were oven dried at 100°C for 72 h and then reweighed. The seasonal green biomass (kg DM ha^{-1}) of each plant species available within each plant community type was determined and then calculated on an individual animal basis for the area occupied by the night-range of each radio-tracked hare.

Diet composition of mountain hares

Diet composition was determined from a sub-sample of 70 faecal samples from 41 different individuals including all 18 radio-collared hares. As often as possible at least two faecal samples consisting of several pellets (minimum DM sample=1.5 g) were collected from each hare, once during the spring and/or summer (February-August) and once during the autumn and/or winter (September-January). Faecal and herbage n-alkane concentrations were determined by gas chromatography using the method of Mayes et al. (1986a). Freeze-dried faecal and plant material was ground to pass through a 1 mm sieve. Duplicate samples of faeces (0.5 g DM) and of herbage (1 g DM–1.5 g DM) were treated with 1 M ethanolic KOH solution in stoppered glass tubes for 16 h at

90°C and then extracted with n-heptane before purification through small silica-gel columns. The purified hydrocarbon extracts were analysed on a PU4500 gas chromatograph (GC) (Phillips, Cambridge, UK), fitted with a flame-ionisation detector. The column was a 30×0.75 mm (i.d.) bonded-phase wide-bore capillary, type SBP1 (Supelco, Bellafonte, Pa., USA) and was temperature-programmed from 225–290°C at 6°C per minute. The carrier gas was helium, and tetratriacontane (C_{34} n-alkane) was used as an internal standard. Each sample was extracted in duplicate and each duplicate was injected twice into the GC column. Evidence from captive hares fed a diet of 100% *Calluna* have revealed no systematic variation in the proportion of ingested alkanes recovered in the faeces and consequently no correction for chain length was necessary (Mayes and Dove 2000).

Approximately 90% of the epidermal fragments found in the stomachs of mountain hares in Scotland is made up of *Calluna*, *Vaccinium* and Gramineae, of which *Deschampsia* is the predominant species (Iason and Waterman 1988; Hulbert and Iason 1996). n-Alkane analysis of dietary composition becomes less reliable with high numbers of species mixtures (Mayes and Dove 2000). Therefore only the major plant species among *Calluna*, *Vaccinium*, *Deschampsia*, *Luzula* and *Lolium* known to be available within the night-range of each radio-tracked hare were included in the analysis of the diet of that hare. The proportions of these five different plant species within the diet of individual hares were estimated using an iterative routine (Microsoft Excel Solver) which minimised the sum of squares of the discrepancy between actual faecal alkane level (expressed as a proportion of total alkane content) and that calculated from alkanes in the plant components. Only alkanes in the range C_{25}-C_{35} were used in the calculation, those with chain-lengths less than C_{25} were not used because of their high analytical error (Mayes et al. 1986b).

Seasonal variation in dietary composition was restricted to the log-ratio analysis of the proportion of browse material (*Calluna)* to the total proportion of Gramineae species in the animal's diet. Such analysis eliminates the possibility of generating either type I or type II statistical errors by repeatedly analysing the seasonal composition of all five dietary components (Sokal and Rohlf 1995). Furthermore, the use of log-ratios overcomes the problem of non-independence of dietary components (Aitchison 1986) and all zero values in the denominator or numerator of the log-ratios were replaced with the value 0.01 which was an order of magnitude smaller than the smallest recorded diet proportion. In biological terms, using such a low value is the statistical equivalent of allowing for the possibility of selection for that dietary component but the number of samples obtained were too few to detect it (Aebischer et al. 1993a, b). As ANOVA cannot reliably be used to analyse data sets that are unbalanced or where sample sizes are low, seasonal variation in diet composition was analysed using residual maximum likelihood (REML) (Genstat 5 Committee 1993) on the derived log-ratios with the individual hare entered as the random variable. REML estimates the components of variation over all sources of information and then assigns appropriate weight to comparisons depending on their respective sizes to obtain information on treatment effects. The Wald test was used to test for the main effects of sex, season and habitat and their interactions (Elston 1998). Statistical differences between values were tested using an analogue of the LSD test (Snedecor and Cochran 1980).

Diet composition and diet selection relative to availability by radio-tracked hares

A sub-sample of faecal samples (n=32) were collected and analysed from the 18 radio-tracked hares, permitting analysis of diet selection in relation to forage available within their home range. Diet composition of this sub-sample was analysed using REML and because of the low sample sizes a simple power test was carried out to determine the probability of determining significant differences (Sokal and Rohlf 1995).

Compositional analysis was used to determine if seasonal dietary composition differed randomly from the proportion of each plant species available within the night range of each radio-tracked hare (Aebischer et al. 1993b). Sample size in this test is critical, and at least six individuals are required to show a significant difference from zero at P<0.05 by randomisation (Siegel 1956; Aebisher et al. 1993b). The test statistic used was Wilk's lambda (λ), which was then applied to the formula $-N\ln\lambda$ where N is the number of dietary samples. The result was then compared to the χ^2 value with D-1 degrees of freedom (D=number of plant species components available) and a probability of less than 0.05 indicated non-random dietary utilisation. If significant, the dietary components were then placed into a rank order of utilisation by constructing a ranking matrix based on mean pairwise differences between log-ratios. Departures from random utilisation were then tested by the Student's *t*-test (Aebisher et al. 1993b).

Results

Faecal and herbage n-alkane concentrations

Large differences in the concentrations of odd-chained n-alkanes for *Calluna*, *Lolium*, *Deschampsia*, *Vaccinium* and *Luzula* in June and December were evident (Table 1). The greater the dissimilarity in n-alkane concentrations the greater the resolution of determination of diet composition using faecal analysis. *Calluna* had

Table 1 Concentration (mg/kg DM) of odd chained n-alkanes in the cuticular wax of the five major plant species used in the analysis of diet composition of free-living mountain hares. Winter samples collected in December and summer samples collected in June

Species		Season	n-alkane					
			C25	C27	C29	C31	C33	C35
Gramineae	*Lolium*	Winter	21.1	17.8	47.5	92.5	78.6	14.4
		Summer	18.8	20.0	57.2	82.3	59.2	8.9
	Deschampsia	Winter	21.8	57.1	250.6	480.6	82.4	3.7
		Summer	28.9	66.2	290.4	342.2	27.6	0
Browse/dwarf shrubs	*Calluna*	Winter	18.6	71.1	176.2	649.8	455.8	13.5
		Summer	27.5	96.0	247.2	677.8	434.9	16.2
	Vaccinium	Winter	19.9	48.0	100.0	45.9	68.5	28.4
		Summer	284.4	434.5	543.8	333.8	39.1	0.0
Rush	*Luzula*	Winter	13.9	71.8	100.3	19.3	3.4	0
		Summer	3.8	34.9	71.3	13.8	1.4	2.5

Table 2 Proportion (%) of the five main species in the diet of mountain hares in each month

Month	*n*	*Calluna*		Gramineae Σ *Lolium* and *Deschampsia*		Gramineae comprising							
						Deschampsia		*Lolium*		*Luzula*		*Vaccinium*	
		%	SE	%	SE	%	SE	%	SE	%	SE	%	SE
January	2	59.2	11.0	25.3	4.3	16.9	0.01	8.5	0.5	15.3	4.7	0.0	0
February	8	55.9	10.1	25.6	5.1	14.2	2.1	11.3	2.5	15.6	4.8	2.8	0.2
March	18	72.8	5.8	24.1	4.9	11.9	1.9	12.1	4.8	3.0	1.3	1.2	0
May	5	18.9	5.2	63.8	6.8	30.9	3.4	32.9	6.5	13.7	2.9	3.5	0.5
June	7	30.2	6.0	42.8	6.9	40.1	3.9	2.6	0.1	17.3	4.1	9.6	3.2
July	9	39.9	9.2	43.4	9.1	34.1	9.1	9.4	5.2	5.9	2.7	11.6	3.1
September	11	38.0	8.5	33.4	5.8	19.6	2.4	13.7	3.4	17.8	1.1	10.7	3.8
November	4	53.9	14.4	27.9	9.2	25.2	3.4	2.8	0.1	19.1	4.4	0.0	0
December	6	66.7	7.2	29.2	7.0	8.6	0.3	20.7	4.6	3.5	0.2	0.1	0
%	70	51.0		33.6		21.1		12.6		10.6		4.7	

much higher concentrations of C_{33} than any other plant whereas *Vaccinium* has relatively high concentrations of the shorter chain alkanes especially during mid-summer. For *Deschampsia*, C_{29} and C_{33} predominate and for *Lolium* C_{31} and C_{33} predominate, while *Luzula* has the highest concentration of C_{29} relative to all other alkanes. Apart from *Vaccinium* there was very little seasonal variation in the relative concentrations of alkanes.

Dietary composition of all mountain hares

Of the five plant species used to determine dietary composition using faecal n-alkane analysis, *Calluna* was the major plant species eaten by adult mountain hares throughout the year, while the Gramineae component was dominated by *Deschampsia* (Table 2). Together, *Calluna* and the two main Gramineae species accounted for 84.6% of the diet of hares occupying the mixed land use mosaic of the present study. There was a significant monthly variation in the ratio of *Calluna* to Gramineae in the hare's diet ($F_{6,25}$=3.88, P<0.05), there being a seasonal shift from a diet containing a greater proportion of *Calluna* from September through to March to a diet containing a greater proportion of Gramineae during mid summer (May, June and July). Consequently, the year was divided into the early-breeding season (February and March) during which 60% (*n*=18) of all female hares sampled were pregnant, the peak-breeding season (May to July) during which all female hares sampled (*n*=12) were pregnant, the post-breeding season (September-November) during which no female was recorded as pregnant and the winter season (December and January) which coincided with the period of deep and prolonged snow cover. Males were assigned to those same seasons depending upon date of capture.

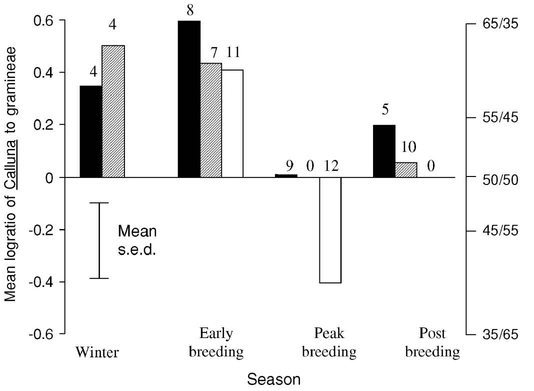

Fig. 1 Mean log ratio of *Calluna* to Gramineae in the diet of adult male and adult female reproductively active and reproductively inactive mountain hares during the winter (December and January), early-breeding (February and March), peak-breeding (May to July) and post-breeding seasons (September and November). Sample size is annotated above each bar. Equivalent percentage ratio of *Calluna* to Gramineae on the right hand axis. *Closed bars* Males, *grey bars* reproductively inactive females, *open bars* reproductively active females

Preliminary analysis of the data revealed that only season had a significant effect on the ratio of *Calluna* to Gramineae in the diet of the hares ($F_{3,26}$=7.4, P<0.05): neither sex nor reproductive status had a significant effect on diet composition (Sex: $F_{1,26}$=1.0; Reproductive Status $F_{1,26}$=0.2, P>0.05). During the peak breeding season, the proportion of *Calluna* in the diet of all hares was significantly less that in the other three seasons. However, upon closer examination, there was no significant seasonal variation in the diet composition of adult male hares and *Calluna* was the dominant component of the diet across all four seasons ($F_{3,13}$=2.1, P>0.05, Fig. 1). For adult females, the ratio of *Calluna* to Gramineae in the diet of reproductively active females during the peak breeding season was dominated by Gramineae (60% to 40%) but during the remainder of the year and regardless of reproductive status, *Calluna* still remained the dominant component of the diet ($F_{3,19}$=7.9, P<0.05, Fig. 1).

Diet composition and diet selection relative to availability by radio-tracked female mountain hares

As only one faecal sample was collected from a radio-tracked female hare during winter, the data for the post

Table 3 Ranking of plant species preferences for radio-tracked female mountain hares during the winter/post breeding season (September through to January), early-breeding season (February and March) and peak-breeding season (May through to July). Data obtained from six hares during the post-breeding/winter season, nine hares in the early-breeding season and seven hares in the peak-breeding season. Unlike letters indicate significant differences within each season

Ranking	Post-breeding/winter season		Early-breeding season		Peak-breeding season	
Highest to lowest						
1	*Deschampsia*	a	*Deschampsia*	a	*Deschampsia*	a
2	*Luzula*	ab	*Lolium*	ab	*Calluna*	b
3	*Calluna*	bc	*Calluna*	bc	*Lolium*	b
4	*Lolium*	bc	*Luzula*	c	*Luzula*	b

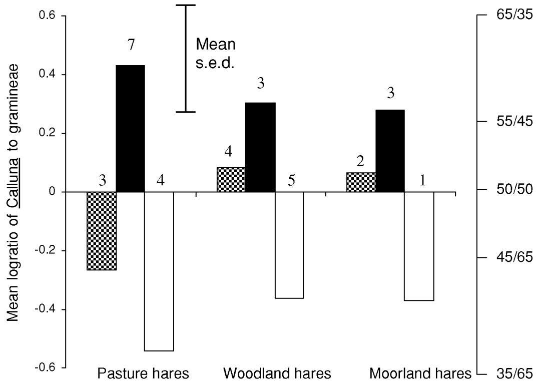

Fig. 2 Mean logratio of *Calluna* to Gramineae in the diet of radio-tracked adult female mountain hares inhabiting the moorland, woodland and pasture habitats during the winter/post-breeding season (September through to January), early-breeding season (February and March), peak-breeding season (May to July). Sample size is annotated above each bar. Equivalent percentage ratio of *Calluna* to Gramineae on the right hand axis. *Stippled bars* Winter/post-breeding, *closed bars* early breeding, *open bars* peak breeding

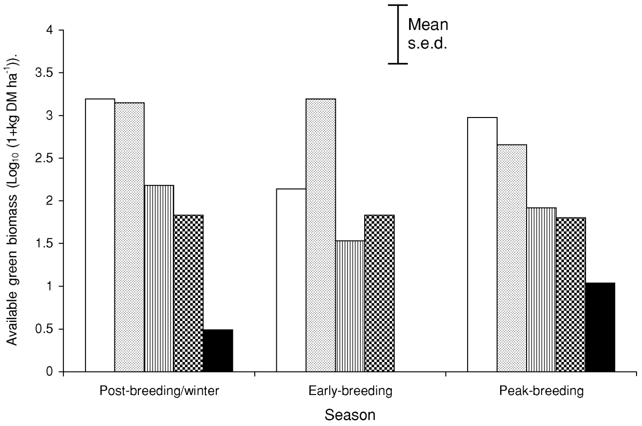

Fig. 3 Available green biomass [Log_{10} (1+kg DM ha^{-1}] of each plant species in the post-breeding/winter season, early-breeding season and the peak-breeding season. *Open bars – Lolium, stippled bars – Calluna, vertical striped bar – Deschampsia, dotted bar – Luzula, closed bar – Vaccinium*

breeding and winter seasons were pooled. There were no differences in the dietary composition of "pasture", "woodland" or "moorland" female hares ($F_{2,23}$=0.2, P>0.05) (Fig. 2). However, the power test revealed that the probability of detecting a significant difference at the 5% level, should true differences of magnitudes of interest exist in the populations, was low (<40%) due primarily to the low sample size.

As for the analysis of all faecal samples from all hares, there were still clear seasonal differences in the diet composition of radio-tracked female hares ($F_{2,23}$=7.9, P<0.05): those in the peak breeding season had a lower proportion of *Calluna* in the diet than at other times of the year. Even although sample size was still low, the observed differences between seasons was high, and consequently the power test revealed that the probability of observing a significant difference at the 5% level was high (>99%).

Although not significant ($F_{8,56}$=0.425, P>0.05), the availability of green biomass (kg DM ha^{-1}) of *Calluna*, *Deschampsia*, *Lolium*, *Luzula* and *Vaccinium* was at its lowest during the early breeding season (Fig. 3). The availability of *Calluna* and *Luzula* varied little during all three seasons but the combined biomass of the Gramineae species was at its lowest during the early breeding season. As *Vaccinium* was virtually unavailable during the early breeding season and furthermore contributed only a small proportion of the diet eaten, it was excluded from the analysis of diet selection relative to availability.

Unlike REML, compositional analysis cannot handle data collected repeatedly from the same individual and, therefore, if an individual hare was sampled more than once during a season, only the data set collected closest to the middle of each season was used. During all three seasons, the early-breeding, peak-breeding and combined post-breeding/winter seasons, the proportion of each plant species in the diet of radio-tracked hares was significantly different from the proportion that each species contributed to the green biomass calculated within the night-range of individual hares (Early breeding: χ^2=13.25, df=3, P<0.05. Peak breeding: χ^2=20.9, df=3, P<0.05. Post breeding/winter: χ^2=14.22, df=3, P<0.05) (Fig. 4). Despite the low relative availability of *Deschampsia*, it was the most preferred species during all three seasons and was selected significantly more than *Calluna* during all three seasons (Table 3).

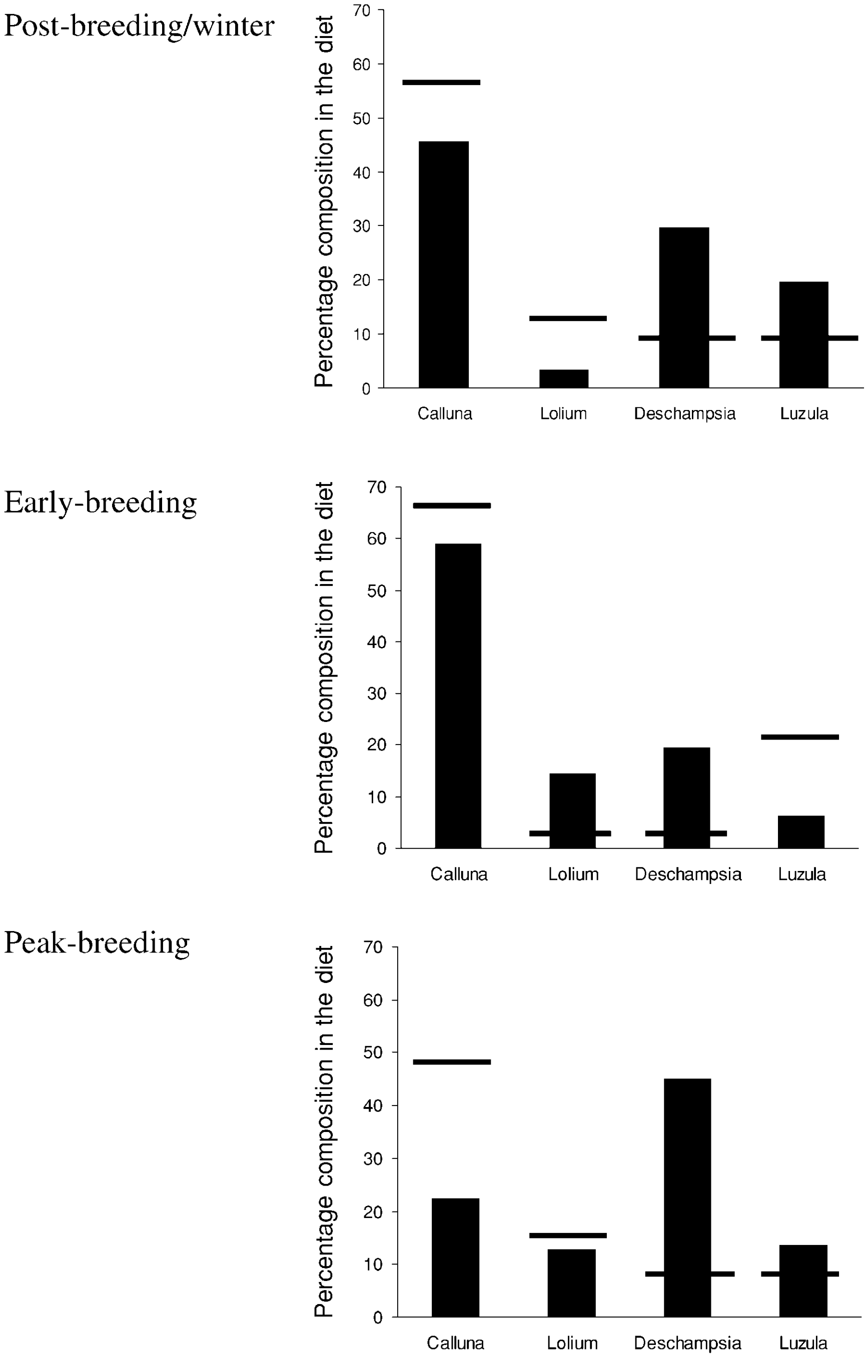

Fig. 4 Diet composition of adult female radio-tracked mountain hares ■ and the plant species composition of green biomass within the feeding range (—) of the same hares, each calculated on an individual basis during the post-breeding/winter season (September through to January), the early-breeding season (February and March) and the peak-breeding season (May through to July). Values are percentage means from six hares during the post-breeding/winter season, nine hares in the early-breeding season and seven hares in the peak-breeding season

Discussion

The applicability of n-alkane analysis to wildlife studies

The use of plant wax alkanes to estimate dietary composition was first developed and validated for studies of domestic ruminants and non-ruminants (Mayes et al. 1994; Dove and Mayes 1996) and latterly for free-ranging herbivores including ungulates and marsupials (Pérez-Barbería et al. 1997; Woolnough 1998). However, whilst the method is reliable for diets containing relatively small numbers of plant components, errors are likely to increase as the number of plant components available and consumed increase (Mayes and Dove 2000). For greatest sensitivity, the total alkane concentrations for each species should be similar but their profiles should differ markedly. Mountain hares were ideal to demonstrate the applicability of n-alkane analysis for estimating the diets of wild herbivores, because of their relatively simple diet (Flux 1970; Iason and Waterman 1988) and because the alkane profiles of the different plant species eaten by hares were sufficiently dissimilar (Table 1). Corrections for differential recovery of individual faecal alkanes of different chain lengths is well established for domestic ruminants (Dove and Mayes 1991) but such measurements in free-ranging herbivores are impossible. However, recent studies have demonstrated that, as for other non-ruminants (pigs and horses), faecal recoveries of some dietary alkanes did not vary with chain length (Mayes and Dove 2000). More research is required to examine faecal recoveries over the total alkane spectrum and for different plant species although studies in sheep suggest that differences between plant species in the faecal recoveries of individual alkanes are unlikely (Mayes et al. 1986b). Theoretically therefore, the major advantage of the use of alkanes is that it makes feasible the characterisation of relatively simple diets for free-ranging herbivores and in this study we have demonstrated the potential of the technique for repeated dietary sampling of known individuals.

Seasonal variation in dietary composition of an intermediate feeder

This study confirms that female mountain hares switch between a browsing strategy in winter with a diet comprising mainly *Calluna* to a grazing strategy in summer with a diet comprising mainly Gramineae (Flux 1970; Iason and Waterman 1988) and, on an annual basis, mountain hares would be considered as an intermediate feeder (sensu Hofmann 1989). Indeed, this intermediate feeding strategy would appear to be more noticeable in the female of the species with the proportions of the two major plant groups – *Calluna* and Gramineae almost completely reversed between the late winter/early breeding months and the peak breeding months in summer. Reproductively active females have high nutrient requirements (Robbins 1983) and are more sensitive to selecting a diet of inferior quality. The reduction in the dietary proportion of *Calluna* in summer and corresponding increase of more highly digestible Gramineae (Kay and Staines 1981) by reproductively active female mountain hares, serves to reduce their intake of plant secondary compounds which are present in *Calluna* in high concentrations (Jalal et al. 1982; Iason et al. 1993). Such compounds may be toxic or act as digestion inhibitors to many mammalian herbivores (McArthur et al. 1991) including hares (Sinclair et al. 1988; Iason and Palo 1991). For adult male hares, dietary composition was dominated by *Calluna*, regardless of season, although the proportion of *Calluna* in the diet was least during the peak breeding season. Even though male steroid production and hence metabolic activity is at its peak (Lincoln 1976; Küderling 1979) during early and peak breeding seasons, the specific nutrient requirements are still less than females who require high protein and energy for gestation and lactation (Robbins 1983). Consequently it is perhaps not surprising that even during periods of intense reproductive activity, males select a diet inferior to that of females. Indeed at this time in the reproductive cycle of hares, females are most probably selecting for food whereas males are selecting for females (Trivers 1972). The role of mating systems and energetic costs of males and females reproductive and foraging behaviour requires further investigation.

The implications of a seasonally-enforced inferior diet can be severe as growth rate and body weight of herbivores, including lagomorphs, are positively related to diet quality (Keith and Windberg 1978; Robbins 1983; Pehrson and Lindlöf 1984). In lagomorphs, such limitations are considered to be related to digestive constraints, particularly around the period of dietary change from a Gramineae-dominated diet to one dominated by browse species during mid- to late autumn (Iason and Van Wieren 1999). Autumn is also one of the main periods of juvenile mortality in mountain hares (Iason 1989). Nevertheless, once adapted to a browse diet, mountain hares do not appear to be nutritionally limited by the lower quality browse forage and indeed, Flux (1970) observed an increase in the condition of mountain hares during the winter months. But why should herbivores, such as mountain hares, adopt an intermediate feeding strategy? During the winter months in the boreal habitats of Scandinavia and *Calluna*-dominated hillsides of Scotland and coastal islands of Sweden, the quality and availability of Gramineae can be extremely unpredictable. Senescence and prolonged periods of heavy and deep snowfall can severely restrict the availability of Gramineae species to grazing herbivores. Although hares are known to dig snow craters in winter to enable feeding at ground level (Gilbert 1990), mountain hares will generally forage on browse species such as *Salix* spp, *Betula* spp. and *Calluna* protruding above the snow (Hulbert and Andersen 2001). Even though the hare has adopted a browsing feeding strategy during the winter months it is still preferentially selecting Gramineae species wherever and whenever they are available. We speculate that for the mountain hare, a seasonally-mediated intermediate feeding strategy is more likely to be driven by the need to be flexible at a time of extreme unpredictability in forage quality and availability.

Are intermediate feeders reluctant browsers?

Hofmann (1968, 1973, 1989) suggested that intermediate feeders could either vary their diet between a grazing or a browsing strategy on an seasonal basis or select a mixed diet throughout the year. Such dietary selection in herbivores is considered to be facilitated by the availability of alternative food sources (Milner and Gwynne 1974). However, regardless of habitat occupied and consequent green biomass availability, the dietary composition of mountain hares was consistent and did not vary between individuals occupying the three different habitats in the present study – moorland, woodland or pasture. For herbivores in general, foraging strategies are considered to be determined by a hierarchical decision process which takes place at different levels: the regional level, landscape level, plant community level down to the level of individual plant or plant part (Senft et al.

1987). In the present study and for other taxa including ruminants and non-ruminants (Duncan 1983; Pérez-Barbería et al. 1997), the foraging strategy of the mountain hares is evidently determined at the level of plant species or even plant part. Indeed mountain hares, which are considered conspecific with the Arctic hares *L. arcticus* and *L. othus* (Corbett 1986; Corbett and Hill 1986) have a circumpolar distribution and are predominantly a species of mixed forest habitats, although in Scotland and on the coastal islands of Scandinavia, mountain hares are traditionally associated with open heather moorland while in Ireland, they occupy moorland and all other habitats down to sea level (Walker and Fairley 1968; Watson et al. 1973; Angerbjörn 1981; Wolfe et al. 1996). In all habitats and in all regions, mountain hares generally ingest a browse dominated diet in winter and a diet dominated by Gramineae in summer (Walker and Fairley 1968; Flux 1970; Pulliainen and Tunkkari 1987; Johannessen and Samset 1994). However, in the present study, diet composition relative to availability was quantified and although the overall selection of Gramineae and in particular *Deschampsia* and avoidance of *Calluna* in females corresponded with the peak in the relative availability of green grass biomass during the peak breeding season, Gramineae were still preferentially selected over *Calluna* during the remainder of the year. Indeed during the early breeding season when the availability (Fig. 3) and the quality of Gramineae are at their lowest (Kay and Staines 1981), the ratio of Gramineae in the diet to Gramineae available was greatest (Fig. 4). So although the relative importance of *Calluna* browse in the diet of mountain hares increases over winter, mountain hares are still preferentially selecting Gramineae to eat. As for other boreal lagomorphs (Sinclair et al. 1982; Smith et al. 1988), mountain hares are highly selective in their choice of diet and avoid their most abundant food source: *Calluna*. Therefore, and in conclusion, seasonal browsers (such as mountain hares) are likely to be reluctant browsers, and only eat browse because there are insufficient higher quality food items such as Gramineae available.

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